New and Noteworthy Venezuelan Glanapterygine Catfishes (Siluriformes, Trichomycteridae), with Discussion of Their Biogeography and Psammophily

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CONTENTS

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ABSTRACT

Four new species of the trichomycterid subfamily Glanapteryginae are described from the Río Orinoco basin of Venezuela. Two new species each in *Pygidianops* Myers 1944 and *Typhlobelus* Myers 1944 represent the first documented occurrence of these genera in Venezuela, and for *Pygidianops* the first occurrence outside the Río Negro basin. The new species were captured from sand-bottom habitats in two disparate locations in the Orinoco River basin and display a remarkable suite of reductive features, such as loss of eyes, fins, and pigment, and reductions or absence of laterosensory canals and odontodes. *Pygidianops cuao*, n.sp. from the Río Cuao, a clear-water tributary of the upper Orinoco River, is diagnosed from its congeners by the presence of diminutive eyes and a triangular skin flap at the corner of the mouth. *Pygidianops magoi*, n.sp., known from near the delta of the Orinoco River, is diagnosed from its congeners by the absence of pectoral and anal fins, presence of four laterosensory pores, and nine or ten caudal-fin rays. *Typhlobelus guacamaya*, n.sp. from the Río Cuao is diagnosed relative to its congeners by the presence of three branchiostegal rays, posterior naris absent, lack of pleural ribs, and is further distinguished from both *T. ternetzi* and *T. macromycterus* by the absence of eyes and from *T. lundbergi* by the presence of three laterosensory canal pores. *Typhlobelus lundbergi*, n.sp. from the lower Orinoco is diagnosed by the presence of four laterosensory canal pores and further distinguished from *T. ternetzi* and *T. macromycterus* by the absence of eyes. We review the characters useful in diagnoses of *Pygidianops* and *Typhlobelus* among trichomycterid catfishes and discuss morphological patterns in the diversification of the Glanapteryginae. Species of *Pygidianops* and *Typhlobelus* are known only from the rivers draining the Guyana and Brazilian shields, yet within these areas they occupy all major water types. Such broad ecological range suggests that the geographic distribution of species of these two genera are not limited by water type. That observation, plus their common occurrence in the ubiquitous shallow sand-bottom habitats of the larger rivers of the shield regions of northern South America, indicate that species of *Pygidianops* and *Typhlobelus* may be expected to occur throughout the entire Amazon and Orinoco basins. The evolution of habitat preference in glanapterygines seems to follow a trend toward increased specialization for interstitial environments. The degree of psammophilic adaptation in species of *Pygidianops* and *Typhlobelus* is remarkable, without parallel in siluriforms and perhaps in any other freshwater fishes. We describe the physical characteristics of the sand and review the suite of morphological specializations for life in interstitial sand that are shared by these species, such as loss or reduction of certain structures and presence in these species of paired metapleural keels along the ventral edges of the abdomen formed by a long ridge of stiffened integument, underlain by well-differentiated medial infracarinalis muscles, that are superficially similar to the metapleural folds of sand-dwelling cephalochordates and other interstitial organisms.

INTRODUCTION

The siluriform family Trichomycteridae is widely distributed throughout the Neotropics and includes perhaps the widest range of trophic adaptations known within any single catfish family assemblage. Apart from the typical free-living, generalized predators of small invertebrates, the rather atypical tro-

phic modes represented among trichomycterid species include the parasitic hematophagous "candirus" of the subfamily Vandeliinae and lepidophagous and muciphagous species of Stegophilinae (Machado and Sazima, 1983), necrophagous species of the subfamily Pareiodontinae (Goulding, 1979, 1980), and the recently discovered and partly algivorous species of the subfamily Copiodontinae (de Pinna, 1992). The range of both ecological habitats and elevations occupied by members of the family rivals the range of trophic specializations represented, and includes species restricted to elevations above 4000 m in the Andes (Arratia and Menu-Marque, 1984; Fernández and Vari, 2000; Fernández and Schaefer, 2003), Andean lakes, off-shore coastal islands (Fernández and Schaefer, 2005), lowland species known only from large rapids (Myers, 1944), leaf-litter puddles, and the bottom of torrential rivers (Arratia, 1998).

Representatives of the poorly known subfamily Glanapteryginae, a group currently comprising four genera and nine species, include some of the most bizarre morphologies and extreme reduction of features thus far known among members of the Siluriformes. The subfamily was described by Myers (1944) to include two new genera and species, *Pygidianops eigenmanni* and *Typhlobelus ternetzi*, plus the previously described *Glanapteryx anguilla* Myers, 1927, all captured from a single locality in the upper Rio Negro of Brazil. No new glanapterygines had been discovered for more than four decades, until de Pinna (1988) described a new genus, *Listrura*, with two species from southeastern Brazil, representing the first record of glanapterygine occurrence outside the Amazon River basin. Costa and Bockmann (1994) based their description of *Typhlobelus macromycterus* on a single specimen from the Rio Tocantins of Brazil. A new species of *Glanapteryx*, *G. niobium*, was described by de Pinna (1998a) from the Rio Negro of Brazil. Landim and Costa (2002) described *Listrura tetraradiata*, a glanapterygine with numerous plesiomorphic features, from coastal streams of Rio de Janeiro State, Brazil. Most recently, de Pinna and Wosiacki (2002) reported on still another species of *Listrura*, *L. boticario*, from southern Brazil. Monophyly

of glanapterygines is supported by five synapomorphies involving reductions in the fins, caudal skeleton, and laterosensory system (de Pinna, 1989). *Glanapteryx* was proposed by de Pinna (1989) as the sister group to a clade composed of *Pygidianops* and *Typhlobelus*, with *Listrura* the sister group to those three.

The genera *Pygidianops* and *Typhlobelus* are the most highly modified glanapterygines, and species of both genera share extreme reduction of pigmentation, loss of dorsal fin, loss or extreme reduction of pectoral fins, reduced laterosensory canal, and complete loss of eyes in some species. Both genera are markedly miniaturized, yet retain a relatively well-ossified skeleton comparable in both bone differentiation and degree of calcification to that observed in larger trichomycterids. Along with *Glanapteryx anguilla*, the type species of both genera were collected at the same time and place, namely, February 1, 1925, at the rocky pools below the São Gabriel Rapids on the upper Rio Negro, Amazonas State, Brazil. Their small size and occurrence in atypical habitats are probably most responsible for the fact that glanapterygines are rarely collected and currently represented in collections by few specimens. However, recent new collections indicate that glanapterygines are more widely distributed than previously thought. For example, Nico and de Pinna (1996), following upon the report of de Pinna (1989), reported on additional populations of *Glanapteryx* in the Río Orinoco basin of Venezuela. Recent collections made in Guyana by J. Armbruster, M. Sabaj, and colleagues have revealed additional populations of *Typhlobelus* and *Pygidianops*, perhaps representing additional undescribed species.

For similar reasons, a more widespread distribution for both *Pygidianops* and *Typhlobelus* has been suspected for some time, yet unconfirmed. We report herein the existence of four new glanapterygine species from the Río Orinoco basin of Venezuela, two new species each in *Pygidianops* and *Typhlobelus*, from two geographically distant locations. One new species each of *Pygidianops* and *Typhlobelus* was collected by one of us (JNB et al.) during the 1979 trawling expedition of the R/V Eastward in white wa-

ter of the Orinoco River delta. After a 0.5 m plankton net, which was being towed behind the boat, inadvertently struck the bottom of the river, specimens of both species were discovered among the coarse sand and gravel that was recovered. An additional new species of each genus was collected by three of us (FPR, SAS, JNB) during a joint expedition in 2001 to the Río Cuao, a clear water tributary of the Río Sipapo, itself a western Guyana Shield tributary of the upper Orinoco River of Amazonas State, Venezuela. These collections represent the first documented occurrence of *Pygidianops* and *Typhlobelus* from Venezuela and, for *Pygidianops*, the first occurrence of the genus outside the Rio Negro basin. All previously described *Typhlobelus* species possess diminutive eyes, whereas the two new species lack eyes entirely. Conversely, the previously described *Pygidianops eigenmanni*, along with one of the new Orinocoan species, lack eyes, while the new species from the Río Cuao has eyes present, although diminutive. The possibility that these new species are juveniles of other recognized species has been considered and rejected based on their well-ossified skeletons and the apparent presence of mature gonads.

In this paper, we diagnose and describe the four new species of *Pygidianops* and *Typhlobelus* from the Río Orinoco system. Keys are provided as an aid to the identification of all species of the two genera. We conclude with a discussion of the biogeographic implications and their psammophilic ecology.

METHODS

Due to the minute size of the taxa treated herein, obtaining morphometric data was problematic and made more difficult by the absence of various fins and eyes, thereby precluding the use of certain traditional landmark reference points. The lack of integument pigmentation also makes the visualization of superficial traits, such as the nares, extremely difficult under optical microscopy. In view of those particulars inherent to the morphology of the species, and in order to provide a standardized future reference for obtaining morphometric data from species of *Pygidianops* and *Typhlobelus*, we here define a set of measurements that are relevant in taxonomic descriptions of those fishes. Most measurements involve distances that are too small to be obtained with calipers and were instead taken using an ocular micrometer fitted to a stereomicroscope. Thus, they are measured as projections rather than straight-line distances. Standard length (SL) was measured with the micrometer for purposes of proportional values, but with digital calipers for absolute values in mm given in lists of material. During measurement, specimens were positioned in ethanol under a glass microscope slide, which served to maintain orientation, straighten and compress the specimens onto the viewing plane, and thereby minimize measurement error.

In addition to standard length, the following measurements were obtained: *caudal peduncle length*—from posterior margin of anus to middle of posterior margin of hypural plate; *body depth*—maximum vertical distance through anterior margin of anus, excluding fleshy dorsal-fin fold, when present; *head length*—from rostrum tip to posterior margin opercular flap at pectoral-fin origin; *head width*—maximum distance perpendicular to longitudinal axis through posterior tip of opercle; *prenasal length*—from rostrum tip at midline to anterior base of nasal barbel; *rostrum length*—from snout tip to anterior mouth margin; *rostrum width*—horizontal maximum through mouth corners; *internarial width*—between anterior margins of nasal barbel bases; *preanal length*—from rostrum tip at midline to base of first anal-fin ray; *preproctal length*—from rostrum tip to anterior margin of anus. Data for rostrum length and prenasal length were excluded for specimens having a damaged or distorted rostrum.

Because all fin rays in *Pygidianops* and *Typhlobelus* species are unbranched and unsegmented (except as noted below), counts for the caudal fin included those rays directly associated with the hypural plate. Anal-fin ray counts included all rays with a corresponding pterygiophore, and the posterior closely set rays were counted separately. Laterosensory canal pores were counted on wet specimens in air; visualization was aided by directing a jet of compressed air onto the structures. Vertebral counts and the vertebral

association of the first anal-fin pterygiophore were taken from radiographs and cleared and stained specimen preparations and include all free vertebra (those incorporated into the Weberian complex not counted) plus the ural complex counted as a single element.

Osteological preparations (denoted "c&s") were made following Taylor and Van Dyke (1985). One specimen of each species was critical point dried, gold coated, and examined using a Hitachi S-4700 scanning electron microscope. Histological preparations were made from 4 μm serial sections that were imbedded in Paraffin and stained with Mason's trichome. Drawings were prepared using a camera lucida attached to a stereomicroscope. In the listing of material examined from the R/V Eastward collections, distance from the buoy marking the ocean/river mouth are indicated in nautical miles for each collections station. Size fractions for Río Cuao sediment were determined by passing a wet sample through a series of sieves of progressively smaller pore openings, and the material collected on each sieve was quantified by volume displacement, described, and measured using an ocular micrometer fitted to a stereomicroscope.

INSTITUTIONAL ABBREVIATIONS

AMNH American Museum of Natural History, New York
CAS California Academy of Sciences, San Francisco
INPA Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
MBUCV Museo de Biologia, Universidad Central de Venezuela, Caracas
MNRJ Museu Nacional, Rio de Janeiro, Brazil
MZUSP Museo de Zoologia, Universidade da São Paulo, São Paulo, Brazil
SU former Stanford University collections, now housed at CAS

COMPARATIVE MATERIAL EXAMINED

Pygidianops eigenmanni SU 36557 paratypes (3:12.3–18.4 mm SL), CAS 11121 paratypes (7:10.5–13.6 mm SL) Brazil, Amazonas, Rio Negro, rock pools below rapids at São Gabriel, C. Ternetz, 1 Feb. 1925. *Pygidianops* sp. INPA 12427 (5) Brazil, Amazonas, Igarapé do Acará (tributary of the Rio Tarumã, Rio Negro basin), A. Kirovsky and M. de Pinna, 10 Nov. 1996. *Typhlobelus ternetzi* SU 36558 paratype (25.3 mm SL) Brazil, Amazonas, Rio Negro, rock pools below rapids at São Gabriel, C. Ternetz, 1 Feb. 1925. *T. macromycterus* MNRJ 12129 holotype (21.9 mm SL) Brazil, Pará, Rio Tocantins near Tucuruí, L. C. Alvarenga, Sept. 1984. *Typhlobelus* sp. INPA 12929 (5) Brazil, Rio Xingu at Arroz Cru, near Senador José Porfírio, J. Zuanon, 7 Oct. 1996.

RESULTS

KEY TO THE SPECIES OF *PYGIDIANOPS* Myers, 1944

1A. Anal and pectoral fins absent; caudal fin with nine or ten rays associated with hypural plate; four laterosensory pores; lower jaw pointed in ventral view, two mandibular rami forming acute angle at midline; distance between middle of lower jaw and anterior margin of rostrum larger than mouth width; rostrum less wide than head width .... *P. magoi*, n.sp.
1B. Anal and pectoral fins present (the latter as a short one-rayed flap); caudal fin with 12 to 14 rays associated with hypural plate; six laterosensory pores; lower jaw forming continuous curve in ventral view; distance between middle of lower jaw and anterior margin of rostrum smaller than mouth width; rostrum as wide as, or wider than, head width 2
2A. Eyes present; triangular skin flap at mouth corner; maxillary and rictal barbels extending posteriorly beyond vertical through base of pectoral fin; nasal barbel extending posteriorly to posterior half of pectoral fin or longer ... *P. cuao*, n.sp.
2B. Eyes absent; no triangular skin flap at mouth corner; maxillary and rictal barbels posteriorly not reaching vertical through base of pectoral fin; nasal barbel reaching posteriorly to base of pectoral fin or shorter ....
.... *P. eigenmanni* Myers,1944

Pygidianops cuao, new species
Figures 1, 2; Table 1

HOLOTYPE: MBUCV-V-30917 (18.70 mm SL) Venezuela, Estado Amazonas, Río Cuao at Raudal Guacamaya, 8.1 miles upstream from Raudal El Danto, 05°07.71′N, 67°31.53′W, SAS01–03, F. Provenzano, S.A.
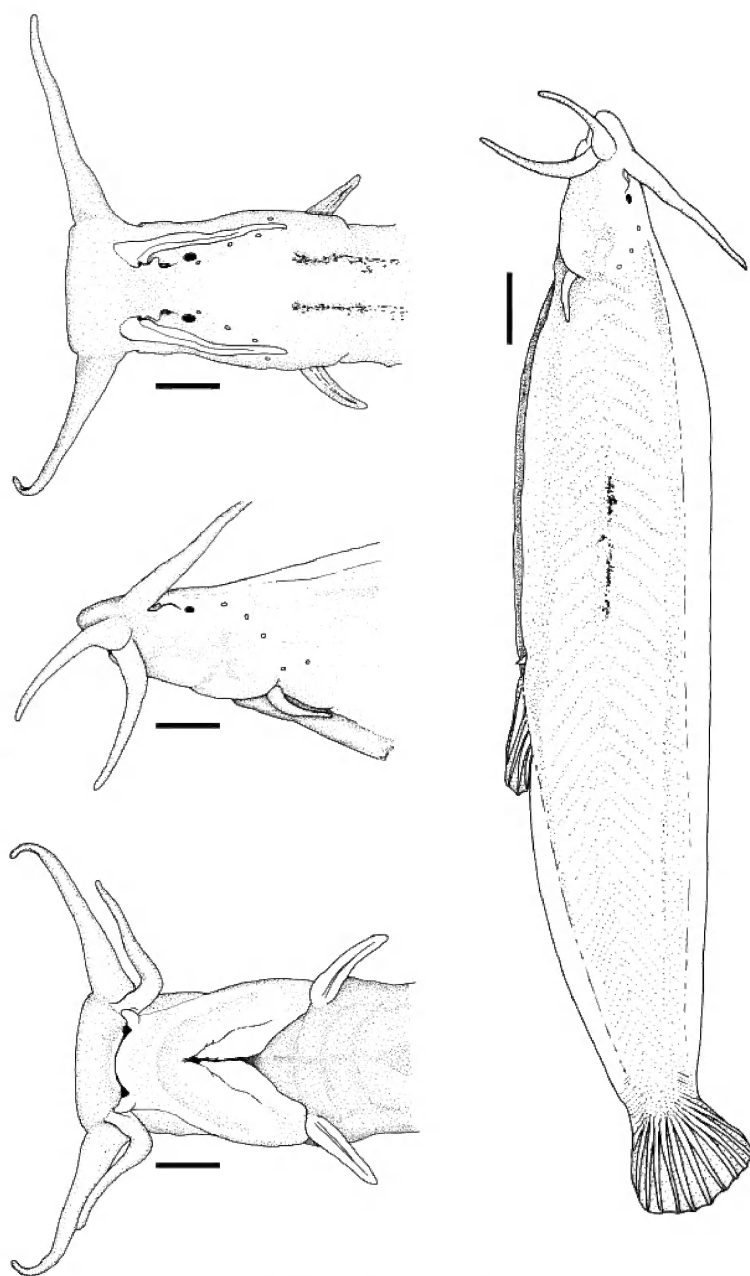
Fig. 1.   *Pygidianops cuao*, holotype, MBUCV V-30917, 21.06 mm SL, Venezuela, Estado Amazonas, Río Cuao at Raudal Guacamaya, 8.1 miles upstream from Raudal El Danto. Scale bar is 1 mm.

TABLE 1
Counts and Measurements of Holotype (HT) and Paratypes (PT) of New Venezuelan *Pygidianops* and *Typhlobelus* Species
Measurements given as percent head length, unless noted otherwise; mean (median for counts) and standard deviation in parentheses.

| | *Pygidianops* | | | | *Typhlobelus* | | | |
| | *cuao* | | *magoi* | | *guacamaya* | | *lundbergi* | |
	HT	PT (*N* = 18)	HT	PT (*N* = 5)	HT	PT (*N* = 9)	HT	PT (*N* = 4)
Standard length (SL)	18.7	17.0 (2.8)	12.6	12.6 (.81)	22.2	22.3 (3.1)	29.0	25.9 (2.6)
Head length (% SL)	16.8	16.1 (1.8)	18.5	17.4 (1.0)	12.2	11.7 (1.0)	11.0	9.7 (0.6)
Body depth (% SL)	17.5	16.1 (1.4)	14.1	14.0 (2.9)	5.1	5.0 (0.4)	4.6	4.2 (0.7)
Head width	63.5	69.0 (4.0)	54.9	56.9 (4.7)	39.3	39.3 (2.7)	44.8	46.2 (3.4)
Preanal length (% SL)	54.8	58.5 (1.7)	—	—	70.4	70.1 (2.2)	73.1	70.7 (1.3)
Preproctal length (% SL)	51.5	56.3 (1.6)	63.8	61.7 (3.0)	69.7	68.5 (1.9)	71.8	68.9 (1.7)
Caudal peduncle length (% SL)	44.8	44.0 (1.9)	—	—	29.5	29.4 (0.9)	24.8	30.8 (1.4)
Rostrum length	12.7	11.4 (1.7)	17.2	16.4 (3.8)	33.3	35.0 (2.5)	24.5	22.5 (1.8)
Rostrum width	26.3	31.0 (3.7)	18.5	20.7 (2.9)	13.7	15.0 (2.6)	17.2	15.4 (1.8)
Prenasal length	23.2	27.6 (4.3)	24.9	21.2 (2.0)	32.2	34.9 (2.6)	31.3	28.0 (1.3)
Internarial width	26.3	30.4 (5.0)	23.6	23.5 (3.7)	17.4	15.3 (2.9)	18.8	13.7 (4.4)
Caudal fin rays	13	13 (.24)	9	9.5 (.58)	9	9 (0)	10	9 (0)
Anal fin rays	4	4 (.51)	—	—	5	5 (0)	5	5 (0)

Schaefer, J.N. Baskin, A. Rojas (hereafter "PSBR"), 3 March 2001.

PARATYPES (all Venezuela, Estado Amazonas): AMNH 232970 (23:16.59–24.00 mm SL), MBUCV-V-29905 (22: 8.13–21.55 mm SL), MZUSP 82103 (5: 13.4–19.0 mm SL) same data as holotype; MBUCV-V-29843 (1: 20.00 mm SL) Río Cuao, Caño Ceje, 5 minutes upstream by boat from Raudal El Danto, 05°05.86′N, 67°31.37′W, SAS01–02, PSBR, 3 March 2001; AMNH 232978 (11: 12.3–23.15 mm SL), MBUCV-V-29922 (10: 12.41–20.30 mm SL), MZUSP 82104 (3: 10.6–18.4 mm SL) Río Cuao at Isla de Cielo, 21.3 kilometers upstream from Raudal El Danto, 05°11.01′N, 67°31.11′W, SAS01–04, PSBR, 5 March 2001; AMNH 232995 (4: 13.95–19.32 mm SL), MBUCV-V-29933 (4: 14.46–18.22 mm SL) Río Cuao at Raudal Pia Poco, 21.5 kilometers upstream from Raudal El Danto, 05°10.95′N, 67°30.81′W, SAS01–05, PSBR, 6 March 2001; MBUCV-V-29977 (3: 8.12–12.15 mm SL) Río Cuao, approximately 20 minutes by motorboat downstream from base camp at SAS01–4, 05°10.13′N, 67°31.76′W, SAS01–7, PSBR, 7 March 2001; AMNH 233036 (6: 12.25–19.27 mm SL), MBUCV-V-29997 (7: 11.05–17.49 mm SL) Río Cuao at Raudal Paují, approximately 10 minutes by motorboat downstream from base camp at SAS01–4, 05°08.92′N, 67°32.18′W, SAS01–8, PSBR, 8 March 2001; MBUCV-V-30105 (4: 8.80–21.65 mm SL) Río Cuao, approx. 10 minutes by motorboat below Raudal El Danto, 05°02.39′N, 67°33.35′W, SAS01–13, PSBR, 10 March 2001.

DIAGNOSIS: Distinguished from congeners by the presence of diminutive eyes (vs. eyes absent), posterior naris absent (vs. nares bilaterally paired), presence of a triangular skin flap at mouth corner (vs. skin flap absent), dorsal and ventral fin fold deep and extending forward on the head to a vertical through tip of pectoral fin (vs. fin fold shallow, extending forward on head to point approximately two times head length from rostrum tip). Further distinguished from *P. magoi* by presence of six laterosensory pores on head (vs. four pores), presence of pectoral and anal fins (vs. fins absent), presence of 12–13 caudal fin rays associated with the caudal plate (vs. 9–10).

DESCRIPTION: General appearance compact, oblate; head slightly depressed and body compressed, trunk neither cylindrical nor ribbonlike. Dorsal and ventral body profiles gently convex. Dorsal profile of head slightly concave at vertical through opercle, gently convex across occipital region. Outline of head rectangular in dorsal view, greatest width (75% HL) at opercle. Anterior rostrum margin blunt, nearly straight between maxillary barbel bases, rounded in lateral profile. Ventrum between pectoral and anal fins forming shallow sulcus with margin of laterally divergent medial infracarinalis (Winterbottom, 1974) fiber bundles (fig. 3). Three pairs of barbels; all similar in general appearance, robust at base. Maxillary barbel continuous with anterior lip margin; its base slightly depressed. Rictal barbel compressed at base, merging with maxillary barbel base at mouth corner. Nasal barbel distinctly separate, extending posteriorly well beyond pectoral fin origin. Mouth ventral, upper lip a broad fleshy pad, anterior margin of lower jaw convex. Small triangular flap of skin projects from corner of mouth (figs. 1, 2) between lower lip margin and rictal barbel base. Posterodorsal corner of branchial opening located immediately anterior to pectoral fin base, gill membrane continuing anteroventrally, its posterior margin straight to slightly concave, not united across isthmus; five branchiostegal rays. Eyes present, but reduced, appearing as compact spherical mass of darkly pigmented cells below slightly raised transparent skin surface. Spherical pigment mass with dorsal indentation filled with mass of opaque cells, yielding rudimentary eyeball and lens configuration. Nares not juxtaposed or connected, but rather well separated; anterior naris at dorsomesial base of nasal barbel, posterior naris larger, located slightly mesial to and one eye diameter anterior to eye, its opening directed laterocaudad. Laterosensory system reduced to short, wide trunk canal segment posterior to supracleithrum and dorsal to pectoral fin, canal continuing onto head through supracleithrum, pterotic, sphenotic, and frontal to terminate just posterior to eye. Six pores total (fig. 2 top, middle), first (anteriormost) immediately behind eye and homologous with the supraorbital epiphyseal pore ("i6" of Ar-

Fig. 2. *Pygidianops cuao*, paratype, AMNH 232995, 19.2 mm SL, scanning electron micrographs of head. Scale bar is 1 mm.
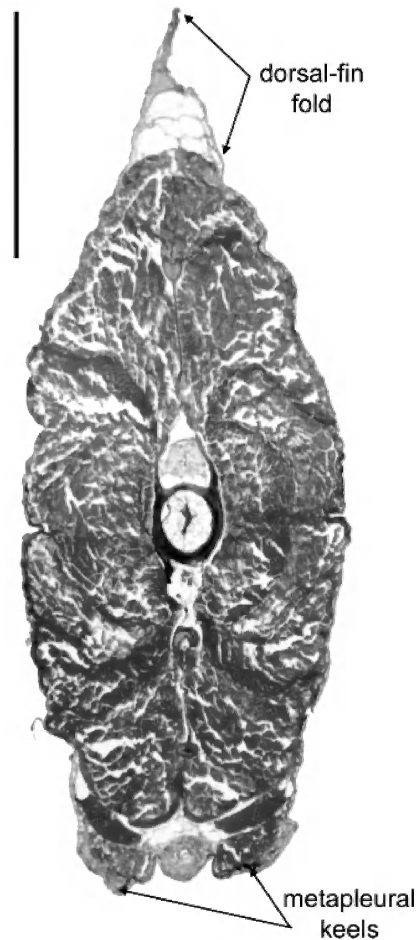

Fig. 3. Histological cross section through the caudal region of *P. cuao* showing dorsal fin fold and ventrally projecting paired metapleural keels (arrows). Scale bar is 1 mm.

ratia and Huaquin, 1995), second at frontal/sphenotic junction and homologous with infraorbital canal branch (canal segment absent), third at pterotic near its anterior margin and homologous with preoperculomandibular canal branch (canal segment absent), fourth at pterotic/supracleithrum junction and homologous with pterotic branch (Schaefer and Aquino, 2000; "L1" of Arratia and Huaquin, 1995), fifth at canal entrance to supracleithrum and homologous with first lateral-line pore, sixth (posteriormost) on trunk at vertical through middle of pectoral fin and representing posterior terminus of short trunk canal.

Dorsal fin absent, dorsum of body with thin, semitransparent fin fold (fig. 3) from head to dorsal margin caudal fin; its greatest depth at vertical through anus, contained three times in body depth. Anal fin present,

4–5 (mostly 4) rays, all unsegmented, unbranched; first ray rudimentary, short, about 0.25 length second ray; first pterygiophore associated with hemal spine of vertebra 17. Ventrum with thin fin fold between base last anal-fin ray to ventral margin caudal fin; its greatest depth about 0.5 times depth dorsal fin fold. Anus and urogenital papilla located immediately anterior to first anal-fin ray. Urogenital papilla length approximately equal to anus diameter, papilla connected to anal-fin base by median ridge of translucent tissue. Caudal fin with 12–13 rays associated with the caudal plate, all unbranched, all but the dorsal and ventralmost rays with 2–4 segments per ray; 4–5 dorsal and 5–7 ventral procurrent rays; spacing between dorsal procurrent rays compacted posteriorly, yielding slightly upturned appearance to caudal fin relative to longitudinal body axis; posterior fin-margin rounded. Pectoral fin present, minute, its length about 0.3 times head length; one unbranched unsegmented ray, fin membrane expanded at base, compressed; distal tip pointed. Pelvic fin and girdle absent.

Jaw teeth unicuspid, blunt; 7–9 mandibular and 6–8 premaxillary teeth per jaw element. Odontodes absent. Trunk myomeres 39–42 (holotype 42), total vertebrae 41.

COLORATION: Pale tan to grey in life. In ethanol, cream white overall, with dense concentration of dark melanophores on occipital region, extending ventral to posterior margin swimbladder capsule; deeper lying melanophores along mesethmoid lateral margin posterior to nasal barbel base and at opercle anterior margin. Trunk with diffuse band of melanophores along dorsal fin-fold base, scattered diffuse line along ventral fin fold, midlateral line with few small, irregularly arranged, discrete clusters of melanophores, ventrum of head and trunk otherwise unpigmented.

DISTRIBUTION: Known only from six collection localities within the Río Cuao drainage basin (fig. 4).

ETYMOLOGY: The specific name is for the Río Cuao, a clearwater tributary of the Río Orinoco and the region of first discovery of the species. Treated as a noun in apposition to the generic name.
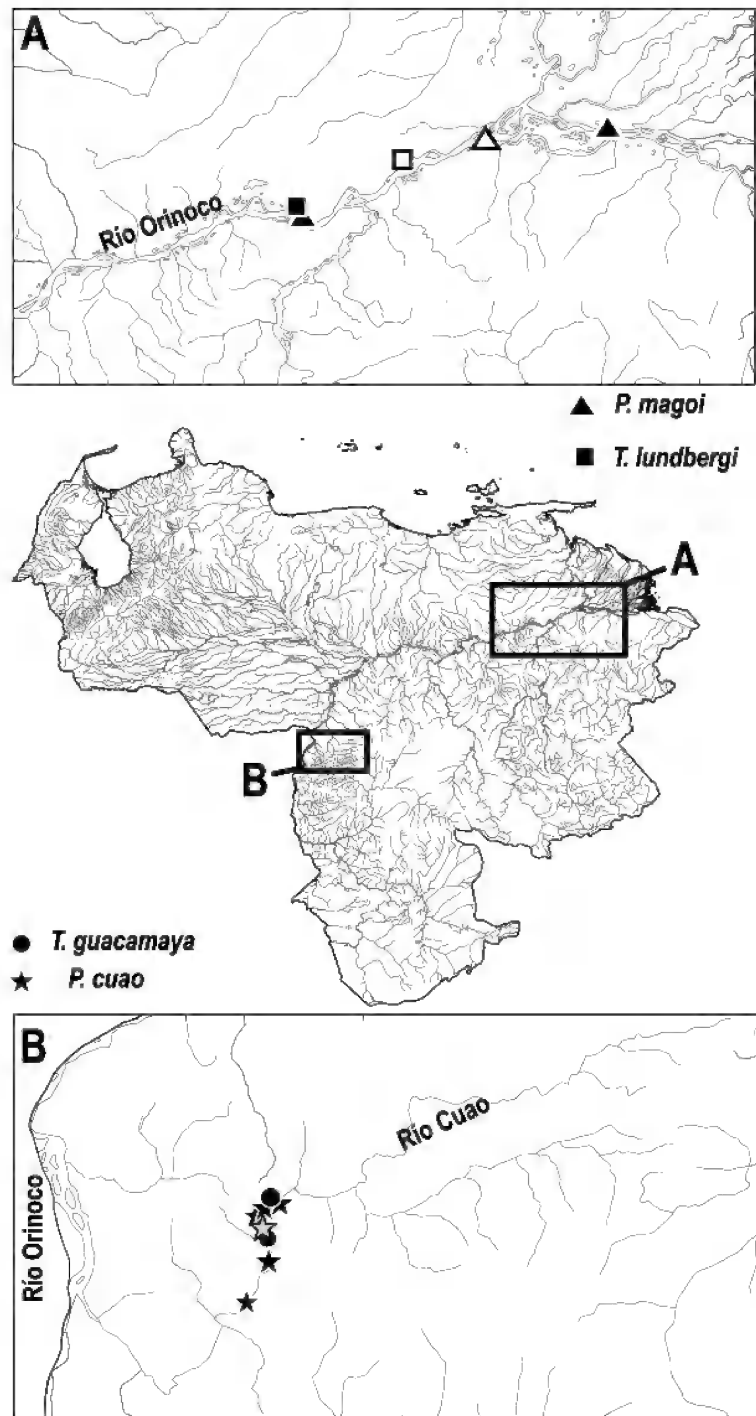
Pygidianops magoi, new species
Figures 5, 6; Table 1

HOLOTYPE: MBUCV-V-31035 (20.0 mm SL) Venezuela, Estado Delta Amacuro, Río Orinoco at Puerto Cabrian, 8°34.8′N, 62°15.9′W, R/V Eastward station 36957, mi 151, field number T-35-79, 10 ft bottom trawl, capture depth 25 m, 13:55 hrs., John G. Lundberg et al., 10 Nov. 1979.

PARATYPES (all from Venezuela): AMNH 233706 (11.71 mm SL), Estado Bolívar, Río Orinoco between Ciudad Bolívar and Puerto Ordaz, 8°20.16′N, 62°57.81′W, R/V Eastward station 36901, mi 203, field number T-12-79, 10 ft bottom trawl, capture depth 18 m, 16:30 hrs., F. Mago-Leccia et al., 7 Nov. 1979; AMNH 233707 (12.69 mm SL) Estado Delta Amacuro, Río Orinoco just downstream from Isla Portuguesa, 8°38′N, 61°49′W, field number T-59-79, mi 116.5, 10 ft bottom trawl, capture depth 30–40 m, 15: 07 hrs., J.G. Lundberg et al., 14 Nov. 1979; AMNH 233708 (11.96 mm SL), MZUSP 84304 (1c&s: 11.4 mm SL) Estado Bolívar, Río Orinoco, 8°18.3′N, 62°56.1′W, R/V Eastward station 36895, field number P-2-79, mi 200.5, 1 m plankton net, capture depth 26 m, 12:55 hrs., H. Lopez-Rojas et al., 7 Nov. 1979; MBUCV-V-31036 (14.5 mm SL) Estado Delta Amacuro, Río Orinoco, just downstream from Isla Portuguesa, 8°38′N, 61°49′W, field number T-61-79, mi 116.5, 10 ft bottom trawl, capture depth 25 m, J.G. Lundberg et al., 14 Nov. 1979; MBUCV-V-31037 (13.4 mm SL) Estado Bolívar, Río Orinoco, Isla Isabella, between Puerto Ordaz and Ciudad Bolívar, 8°19.7′N, 62°56.8′W, R/V Eastward station 36924, field number T-18-79, mi 203, 10 ft bottom trawl, capture

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Fig. 4. Geographic distribution of the Venezuelan Glanapteryginae. Drainage map of Venezuela (center); rectangles depict regions of interest expanded in A and B. **A,** lower Río Orinoco; **B,** Río Cuao. Symbols designate collection localities; some symbols represent more than one lot. Open symbols designate holotype; grey star symbol denotes shared type locality for both *P. cuao* and *T. guacamaya*.
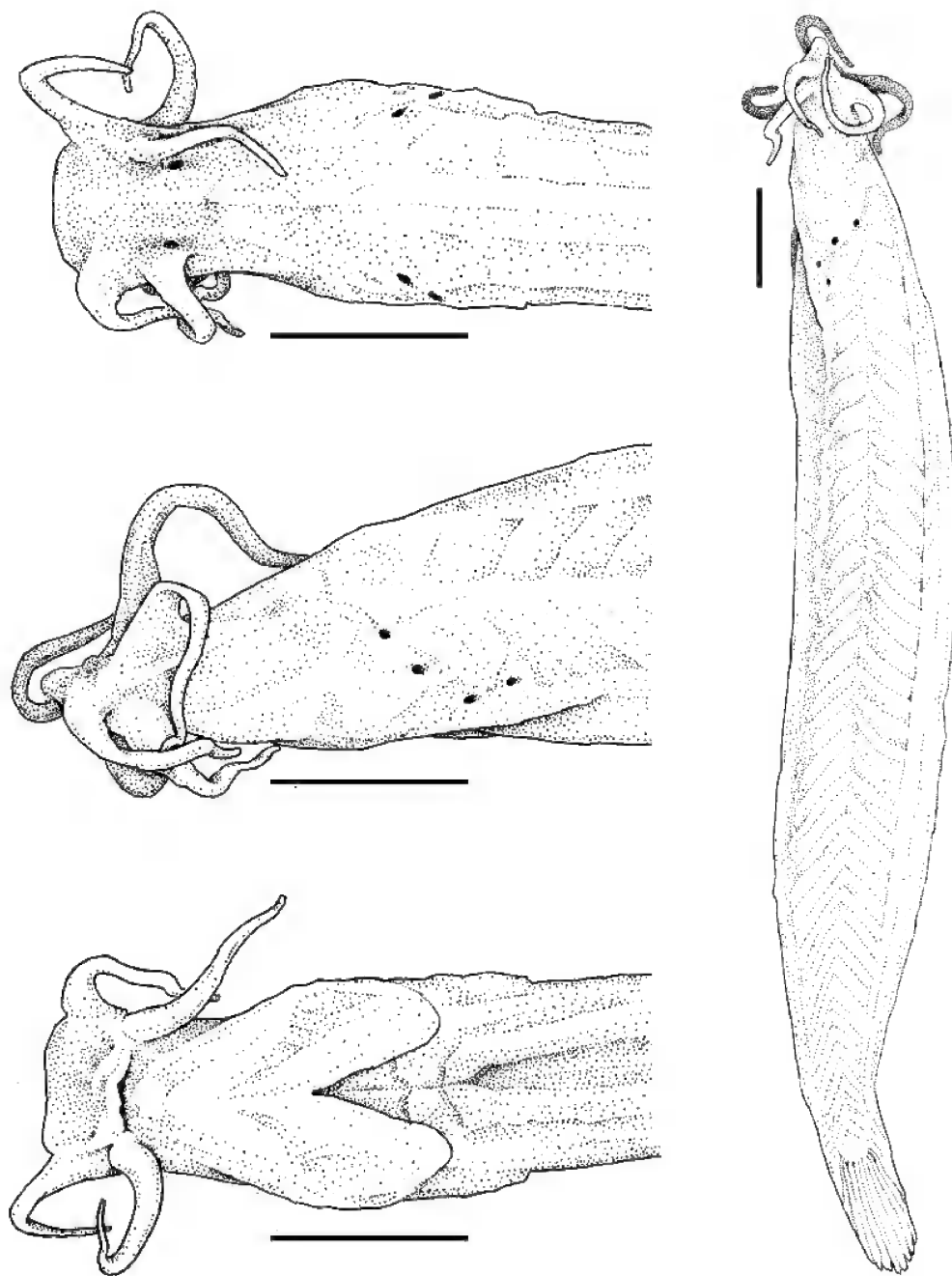
Fig. 5.   *Pygidianops magoi*, holotype, MBUCV-V-31035, 20.0 mm SL, Venezuela, Estado Delta Amacuro, Río Orinoco at Puerto Cabrian. Scale bar is 1 mm. Illustrations by Ian Hart.

Fig. 6. *Pygidianops magoi*, paratype, MZUSP uncat, 11.2 mm SL, scanning electron micrographs of head. Scale bar is 1 mm.

depth 16–19 m, 14:59 hrs., J.N. Baskin et al., 9 Nov. 1979; MZUSP 84303 (2: 15.0–15.3 mm SL), same data as holotype; MZUSP 84306 (15.7 mm SL) Estado Delta Amacuro, Río Orinoco downstream from Puerto Cabrian, 8°34′N, 62°15′W, field number T-36-79,

10 ft bottom trawl, John G. Lundberg et al., 11 Nov. 1979.

DIAGNOSIS: Distinguished from all congeners by the absence of pectoral and anal fins (vs. fins present), posterior naris absent (vs. present, nares bilaterally paired), four laterosensory pores on the head (vs. six), and by presence of 9–10 caudal fin rays (vs. 12–13). Further distinguished from *P. eigenmanni* by the absence of eyes (vs. eyes present, diminutive).

DESCRIPTION: General appearance compressed, slender; head slightly depressed. Dorsal body profile convex. Dorsal profile of head slightly convex across occipital region. Head rectangular in dorsal view, greatest width (64% HL) at opercle. Anterior rostrum margin blunt, broad in dorsal view, nearly straight between maxillary barbel bases. Ventral body profile straight to slightly concave; ventrum forming shallow sulcus between ventral margin of gills and anus.

Three pairs of barbels; all similar in general appearance, size and shape, base slightly wider than shaft. Maxillary barbel continuous with anterior lip. Rictal barbel slender, its base merging with that of maxillary barbel at mouth corner. Nasal barbel compressed, its base wide and flattened; distinctly separate from maxillary barbel, extending posteriorly to posterior opercle margin. Mouth ventral, upper lip a broad fleshy pad; no skin flap at corner of mouth. Branchial opening positioned mostly ventrolateral on head, gill membrane nearly straight ventrally, united across isthmus; four branchiostegal rays. Eyes absent. Naris (anterior) at anterior base of nasal barbel, posterior naris absent. Laterosensory system reduced to short canal segment posterior to supracleithrum; canal continuing onto head through supracleithrum and pterotic to terminate at sphenotic/pterotic junction. Four pores total (fig. 6, middle), i6 and infraorbital canal-branch pore absent; first pore (anterior and dorsalmost) homologous with preoperculomandibular branch located at vertical through operculohyomandibular articulation, second located at pterotic/supracleithrum junction and homologous with pterotic branch (canal segment absent), third at canal entrance to supracleithrum and homologous with first lateral-line pore, fourth (posteriormost) on trunk at vertical

through tip of first neural spine (externally, at division between second and third epaxial myomeres) and representing posterior terminus of short trunk canal.

Dorsal fin absent, dorsum of body with thin fin fold from point approximately three head lengths from rostrum tip to dorsal margin caudal fin; its greatest depth at vertical through anus, contained about 4.5 times in body depth. Urogenital papilla slender, located posterior to anus, length approximately equal to anus diameter. Pectoral, pelvic, and anal fins absent. Caudal fin with 9–10 rays associated with the caudal plate, all unbranched and unsegmented.

Jaw teeth unicuspid; 5–7 mandibular and 5–7 premaxillary teeth per jaw element. Odontodes absent. Trunk myomeres 39 (holotype), total vertebrae 35–41.

COLOR IN ETHANOL: Pale yellow overall, faded; melanophores not apparent.

DISTRIBUTION: Known only from six localities on the lower Río Orinoco mainstem between Ciudad Bolívar and Barrancas (fig. 4).

ETYMOLOGY: The specific name is given in tribute to the late Professor Francisco Mago-Leccia (born Tumeremo, May 21, 1931; died Puerto La Cruz, February 27, 2004), in recognition of his participation in the discovery of the species, his innumerable contributions to the ichthyology of northern South America, and his mentorship and enthusiasm in the study of Venezuelan fishes.

KEY TO THE SPECIES OF *TYPHLOBELUS* MYERS, 1944

1A. Rostrum expanding immediately anterior to its base, then narrowing gradually to tip; margin of rostrum posteriorly overlapping base of maxillary barbel, not continuous with it; posterior naris absent; three branchiostegal rays; no pleural ribs . . . . *T. guacamaya*, n.sp.
1B. Rostrum narrowing gradually from base to tip; margin of rostrum continuous with anterior margin of maxillary barbel; anterior and posterior nares present, separate; four or five branchiostegal rays; one pair of pleural ribs 2
2A. Opercle with one or two distal odontodes; five branchiostegal rays . . . . *T. macromycterus* Costa & Bockmann, 1994

2B. Opercle lacking odontodes; four branchiostegal rays 3
3A. Eye spots present; approximately 60 vertebrae; fin folds on caudal peduncle deeper dorsally than ventrally . . . . *T. ternetzi* Myers, 1944
3B. Eye spots absent; 70 vertebrae; dorsal and ventral fin folds on caudal peduncle equally deep . . . . . . *T. lundbergi*, n.sp.

Typhlobelus guacamaya, new species
Figures 7, 8; Table 1

HOLOTYPE: MBUCV-V-30916 (22.20 mm SL) Venezuela, Estado Amazonas, Río Cuao at Raudal Guacamaya, 8.1 miles upstream from Raudal El Danto, 05°07.71′N, 67°31.53′W, SAS01–03, PSBR, 3 March 2001.

PARATYPES (all Venezuela, Estado Amazonas): AMNH 232974 (3: 20.25–22.20 mm SL, 1 c&s), MBUCV-V-29904 (3: 15.29–24.75 mm SL; 16.31–26.70 mm TL), MZUSP 81770 (3: 23.3 25.6 mm SL) data as for holotype; AMNH 233711 (2: 25.01–25.30 mm SL) Río Cuao at Raudal Pia Poco, 21.5 kilometers upstream from Raudal del Danto, 05°10.95′N, 67°30.81′W, SAS01–05, PSBR, 6 March 2001; MBUCV-V-30006 (23.55 mm SL; 25.19 mm TL) Río Cuao at Raudal Paují, approximately 10 minutes by motorboat downstream from base camp at SAS01–4, 05°08.92′N, 67°32.18′W, SAS01–8, PSBR, 8 March 2001.

DIAGNOSIS: *Typhlobelus guacamaya* is distinguished from all congeners by the presence of three branchiostegal rays (vs. four in *T. ternetzi* and *T. lundbergi*, five in *T. macromycterus*), posterior naris absent (vs. present, nares bilaterally paired), and the lack of pleural ribs (vs. one pair of pleural ribs associated with the first free vertebra). The new species is further distinguished from both *T. ternetzi* and *T. macromycterus* by the absence of eyes (vs. eyes present, vestigial), and further distinguished from *T. macromycterus* by the presence of nine (vs. ten) caudal-fin rays and five (vs. six) anal-fin rays. Of the species from the Río Orinoco basin, the new species is further distinguished from *T. lundbergi* by the presence of three (vs. four) laterosensory canal pores.

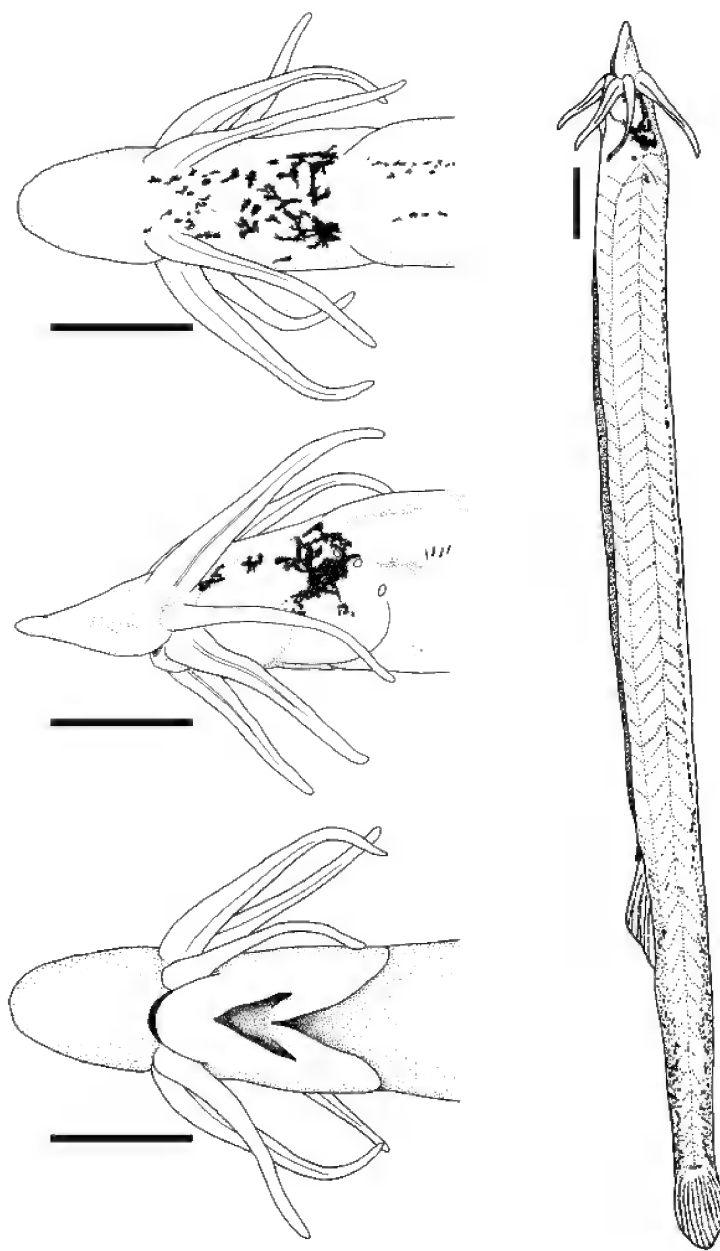DESCRIPTION: Body greatly elongate, slender; greatest body depth at vertical through

Fig. 7.   *Typhlobelus guacamaya*, holotype, MBUCV-V-30916, 22.20 mm SL, Venezuela, Estado Amazonas, Río Cuao at Raudal Guacamaya, 8.1 miles upstream from Raudal El Danto. Scale bar is 1 mm.

Fig. 8. *Typhlobelus guacamaya*, paratype, AMNH 232974, 20.7 mm SL, scanning electron micrograph of head, scale bar is 1 mm.

point halfway between rostrum tip and anal fin origin, 5–6% SL, contained 15–17 times in SL. Dorsal and ventral body profiles straight. Head conical posterior to barbels, head length 10% SL, greatest width at opercle (48% HL), greatest depth 50% HL at vertical through second cranial laterosensory canal pore. Rostrum spatulate, projecting an-

teriorly as broad, thin, depressed disk, slightly upturned near tip, anterior margin smoothly rounded in dorsal view; rostrum length 40% HL. Dorsal profile of head concave behind rostrum tip, straight between nasal barbel and occipital region; ventral profile of head straight. Ventrum between branchial opening and anal fin forming shallow sulcus with lateral margin of median infracarinalis muscle fiber bundles; caudal peduncle compressed, profiles straight.

Three pairs of barbels, all similar in length and general appearance, compressed and expanded proximally, slender and uniramous distally. Maxillary barbel separated from rostral margin by deep groove, rictal barbel juxtaposed between maxillary barbel base and corner of mouth. Nasal barbel positioned on dorsum at horizontal through corner of mouth, connected to dorsum of rostrum by thin vertical skin ridge. Naris (anterior) located at midpoint of nasal barbel base along mesial margin of barbel (fig. 8, top), posterior naris absent. Mouth ventral, upper lip separated from rostrum, its anterior margin concave medially; lower lip broad, anterior margin convex. Branchial opening located along lateral head, posterior margin straight; posterodorsal limit of opening low on head, at horizontal through rostrum, at vertical through posteriormost laterosensory canal pore; gill membranes united across isthmus; three branchiostegal rays. Eyes absent. Laterosensory system reduced to short canal on head, passing through supracleithrum and pterotic; three pores total (figs. 7, 8 middle), first (anteriormost) minute, at vertical through opercle and homologous with preoperculomandibular canal branch, second large, homologous with pterotic canal branch, third (posteriormost) at vertical through posterodorsal corner branchial opening, homologous with first lateral-line canal pore (more posterior trunk canal segment absent).

Dorsal fin absent, dorsum of body with very shallow, thin semitransparent fin fold from head to dorsal margin caudal fin; barely perceptible anteriorly, greatest depth above anal fin. Anal fin present, five rays, all unsegmented and unbranched; first ray longest, first pterygiophore associated with hemal spine of vertebra 36. Ventrum with shallow

thin fin fold from last anal fin ray to ventral margin caudal fin. Anus and elongate pointed urogenital papilla located immediately anterior to first anal fin ray, papilla distinctly smaller in some specimens. Caudal fin with nine rays associated with the caudal plate, all unbranched, unsegmented; five dorsal, three ventral procurrent rays; posterior fin margin rounded. Pectoral fin absent; pelvic fin and girdle absent.

Jaw teeth minute, conical; 6–7 mandibular teeth per jaw element, premaxillaries edentulous. Odontodes absent. Trunk myomeres 56–58 (holotype 58), total vertebrae 51–53.

COLORATION: Pale grey in life. In ethanol, cream white overall, with diffuse scattering of melanophores on trunk, dense concentration of superficial melanophores on dorsum of head from mesethmoid tip to occipital region, deeper lying, darker melanophores on head laterally below pterotics. Thin, bilateral concentration of melanophores along dorsal and ventral midline; on dorsum extending from occipital region to dorsal margin caudal fin, on ventrum extending from anal fin origin to ventral margin caudal fin. Ventrum of head and trunk otherwise unpigmented.

DISTRIBUTION: Known only from three collection localities within the Río Cuao drainage basin (fig. 4).

ETYMOLOGY: The specific name is taken from the name of the rapids on the middle Río Cuao where the first specimens were encountered; treated as a noun in apposition to the generic name.

Typhlobelus lundbergi, new species
Figures 9, 10; Table 1

HOLOTYPE: MBUCV-V-31040 (28.18 mm SL) Venezuela, Estado Delta Amacuro, Río Orinoco at Los Castillos, upstream of east end of Caño Limon, 8°31.2′N, 62°35.1′W, R/V Eastward station 36934, field number T-21-79, mi 161.8, 10 ft bottom trawl, capture depth 35–40 m, 11:27 hrs, J.N. Baskin et al., 10 Nov. 1979.

PARATYPES (all from Venezuela): AMNH 233709 (24.28 mm SL), Estado Bolívar, Río Orinoco between Puerto Ordaz and Ciudad Bolívar, 8°19.9′N, 62°57.4′W, R/V Eastward station 37900, field number T-11-79, mi 203, 10 ft bottom trawl, capture depth 18 m, 15:

55 hrs., F. Mago-Leccia, 7 Nov. 1979; AMNH 233710 (29.77 mm SL), MBUCV-V-31041 (24.77 mm SL), MZUSP 84305 (2, 1c&s: 20.8–22.0 mm SL) Estado Bolívar, Río Orinoco, 8°18.3′N, 62°56.1′W, R/V Eastward station 36895, field number P-2-79, mi 200.5, 1 m plankton net, capture depth 26 m, 12:55 hrs., H. Lopez-Rojas et al., 7 Nov. 1979.

DIAGNOSIS: Distinguished from all congeners by the presence of four laterosensory pores on the head (vs. three). Further distinguished from *T. ternetzi* and *T. macromycterus* by the absence of eyes (vs. eyes present, vestigial); from *T. macromycterus* and *T. guacamaya* by the presence of four branchiostegal rays (vs. five and three, respectively).

DESCRIPTION: Body greatly elongate, slender; greatest body depth 5% SL at vertical through point halfway between rostrum tip and anus. Dorsal and ventral body profiles straight. Head conical posterior to barbels, head length 9–11% SL, greatest width 50% HL at opercle, greatest depth 70–79% HL at vertical through opercle. Rostrum spatulate, projecting anteriorly as depressed, discoid bill or beak; rostrum length from anterior mouth margin to rostrum tip 20–25% HL, its anterior margin elliptical in dorsal view; prenasal length from rostrum tip to nasal barbel base 27–31% HL. Rostrum slightly upturned, dorsal profile of head concave behind rostrum tip, gently convex between nasal barbel and occipital region; ventral profile of head slightly convex. Ventrum forming shallow sulcus margined laterally by median infracarinalis muscle fibers between branchial opening and anal fin origin; caudal peduncle margins straight, ovoid in cross section.

Three pairs of barbels, all similar in length and general appearance, their bases compressed laterally; slender, uniramous distally. Maxillary barbel separated from rostral margin by shallow cleft, rictal barbel base positioned immediately ventral to maxillary barbel base, its anterior margin expanded, continuous with anterolateral corner of mouth. Nasal barbel well separated from maxillary barbel, compressed laterally, its anterior margin thin, extending anteriorly onto rostrum. Mouth ventral, upper lip hardly separated from rostrum; lower lip broad, anterior mar-
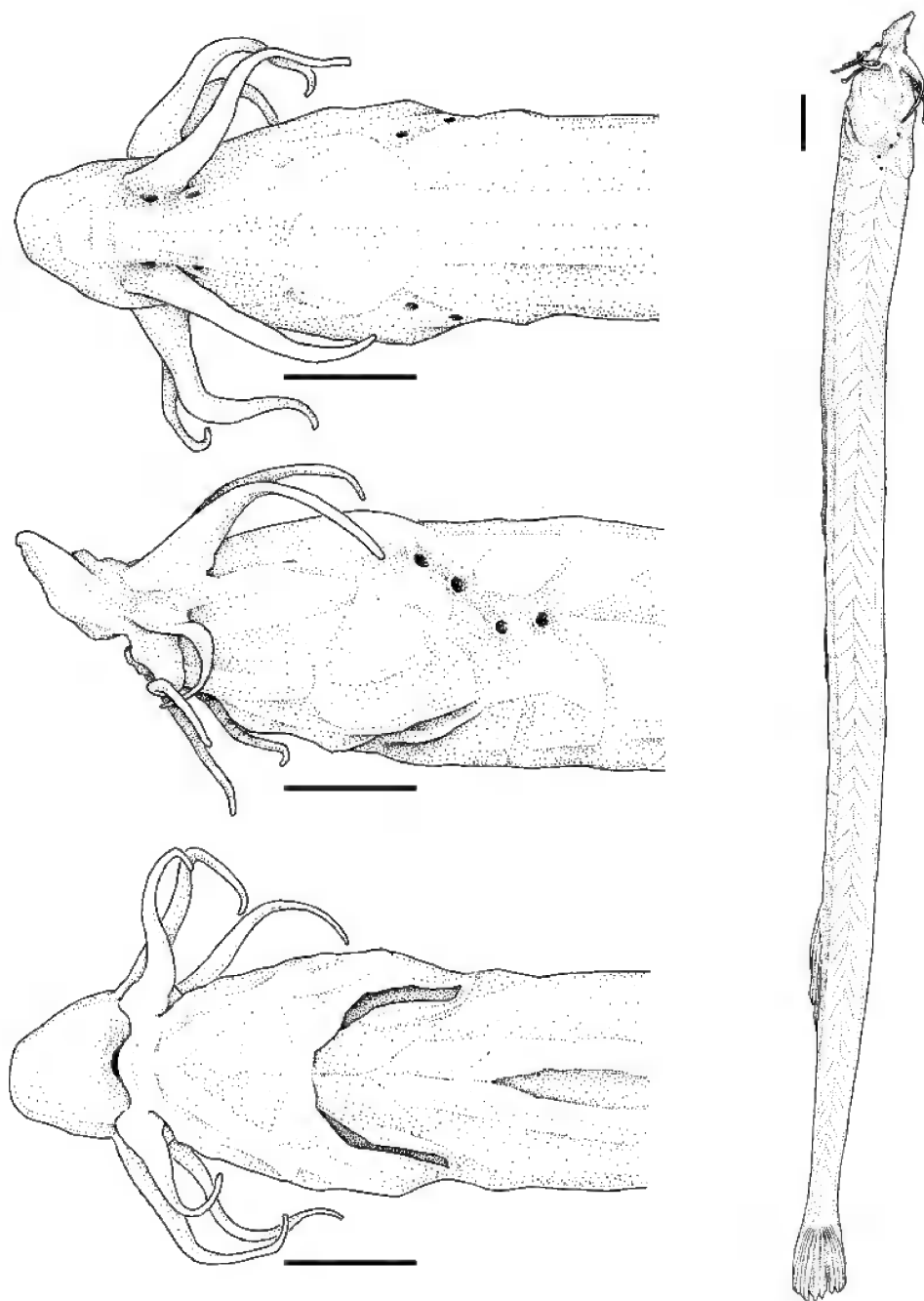
Fig. 9.   *Typhlobelus lundbergi*, holotype, MBUCV-V-31040, 28.18 mm SL, Venezuela, Estado Delta Amacuro, Río Orinoco at Los Castillos, upstream of east end of Caño Limon. Scale bar is 1 mm. Illustrations by Ian Hart.
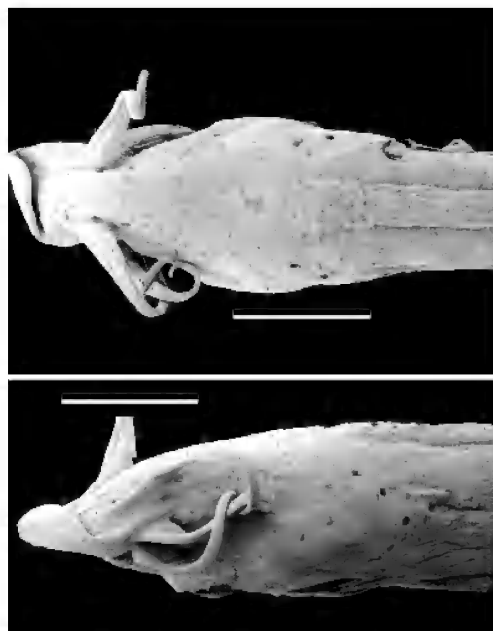
Fig. 10. *Typhlobelus lundbergi*, paratype, MZUSP uncat, 19.1 mm SL, scanning electron micrograph of head, scale bar is 1 mm.

gin convex. Branchial opening low on head, posterodorsal apex at horizontal through lower lip, at vertical through tip of first neural spine; gill membranes united across isthmus, four branchiostegal rays. Eyes absent. Anterior and posterior nares separated (fig. 10, top), anterior naris at middle of nasal barbel base along mesial margin, posterior naris positioned posterior to nasal barbel, separated from anterior naris by distance equal to nasal barbel base length. Laterosensory system reduced to short canal on head, passing through supracleithrum and pterotic; four pores total (fig. 10, bottom), first (anteriormost) large, at vertical through posterodorsal corner of opercle and homologous with preoperculomandibular canal branch (branch absent), second at junction between supracleithrum and pterotic and homologous with pterotic branch, third at canal entrance to supracleithrum and homologous with first lateral-line canal pore, fourth (posteriormost) behind and slightly dorsal to third pore and representing posterior terminus of short trunk canal.

Dorsal fin absent, dorsum of body with thin, extremely shallow fin fold from point two-thirds the distance from rostrum tip to anal fin origin, extending onto dorsal margin of caudal fin; barely perceptible along its entire length. Anal fin present, five rays, all unsegmented and unbranched; first ray longest, first pterygiophore associated with hemal spine of vertebra 35. No ventral fin fold. Anus located anterior to first anal fin ray. Urogenital papilla located closer to anus than to anal fin origin, papilla length approximately equal to anus diameter. Caudal fin with ten rays associated with the caudal plate, all unbranched and unsegmented; five dorsal and four ventral procurrent rays; posterior fin margin rounded. Pectoral and pelvic fins absent, pelvic girdle absent.

Jaw teeth conical, pointed; 5–6 mandibular teeth per jaw element, premaxillaries edentulous. Odontodes absent. Trunk myomeres 52 (holotype), total vertebrae 53–71.

COLOR IN ETHANOL: Cream white overall, without melanophores except for small concentration of faded melanophores on dorsum of head over frontals.

DISTRIBUTION: Known only from three collections localities on the lower Río Orinoco near its delta between Ciudad Bolívar and Los Castillos (fig. 4).

ETYMOLOGY: The specific name is given for John G. Lundberg, in recognition of his contributions to neotropical ichthyology, his efforts during the R/V Eastward cruises and the study of the demersal fish fauna of large rivers.

DISCUSSION

GENERIC DIAGNOSES

Current diagnoses for the genera *Pygidianops* and *Typhlobelus* leave no doubt as to the generic allocation of the new species described herein. The two genera are easily distinguishable from one another on the basis of various traits from external morphology reported in Myers (1944). *Typhlobelus* has a long duck-billed rostrum that protrudes anteriorly well beyond the bases of the maxillary barbels. This is associated with the markedly elongated mesethmoid shaft, which extends anteriorly well beyond the premaxillae and palatines. The rostrum in *Pygidi-*

anops is short and broad, gently convex between the bases of the maxillary barbels in dorsal view. Also, *Typhlobelus* has a much longer body, reflected in the greater number of vertebrae (52–71 vs. 40–43). The original generic diagnoses provided by Myers (1944) included additional distinguishing characters, such as the presence of pectoral fins in *Pygidianops* and their absence in *Typhlobelus*. The opposite was reported for eyes, which are absent in the former and present in the latter. These distinctions, however, do not hold when the new species described herein are considered. For example, *P. cuao* has eyes and *T. guacamaya* and *T. lundbergi* both lack them. Likewise, *P. magoi* lacks a pectoral fin. Myers (1944) also mentioned a difference in dentition (spacing of teeth), which obviously could not be properly examined at that time due to the lack of clearing and staining techniques suitable for such small and delicate specimens.

Internal anatomy provides an additional suite of diagnostic characters for the two genera. A detailed review of the osteology of *Pygidianops* and *Typhlobelus* is beyond the scope of this contribution, but a few particularly conspicuous traits deserve mention. The palatine of *Typhlobelus* species is among the most highly modified of any trichomycterid. It is a small club-shaped bone with its main axis oriented nearly transversely to the neurocranium. This contrasts sharply with the usual trichomycterid palatine, which is large, broad and flat, with its main axis oriented approximately parallel to the neurocranium. The condition in *Typhlobelus* can certainly be considered as apomorphic within the family. The premaxilla of *Typhlobelus* is also highly modified into a thick three-dimensional frame, approximately round in cross section. This is a condition profoundly distinct from the normal catfish premaxilla, which is a flat bone. The structure of the jaws also provides support for the monophyly of *Pygidianops*. In all species of the genus, the premaxilla bears a large dorsal process inserted on the mesial part of its dorsal surface and directed laterally, parallel to the dorsal surface of the bone. In sum, the evidence for the monophyly of *Pygidianops* and *Typhlobelus* seems robust, and there is little question as to the validity of the two genera, as

well as to the respective generic allocation of the new species described herein.

Phylogenetic relationships among glanapterygines are known only in general outline. Among genera currently recognized, it seems certain that the southeastern Brazilian *Listrura* is the sister group to the remainder of the subfamily. *Glanapteryx* is the sister group to *Pygidianops* plus *Typhlobelus* (de Pinna, 1989), all of which occur in the Amazon and Orinoco basins. In addition to that, synapomorphies have been proposed for all individual glanapterygine genera, and it seems that all of them are monophyletic as presently constituted. While monophyly of both *Pygidianops* and *Typhlobelus* seems well corroborated, phylogenetic relationships among their respective species are still unresolved, and data presently available do not suggest any evident hypothesis. Characters so far observed seem to form a largely contradictory mosaic of similarities. Autapomorphies for individual species of *Pygidianops* and *Typhlobelus* are still scarce, but a few are identified in this study. One of the most interesting such characters is the total absence of pleural ribs in *T. guacamaya*. Other species in the genus have one pair of ribs, while species of *Pygidianops* have two pairs. The lack of anal fin in *P. magoi* is also easily hypothesized as autapomorphic, because all species of *Pygidianops* and *Typhlobelus* have one. The only other glanapterygines lacking an anal fin are species of *Glanapteryx*, but they are distant from *P. magoi* in glanapterygine phylogeny, and the conditions are probably convergent. *Pygidianops magoi* is also autapomorphically diagnosed by the loss of mesethmoid cornua, a condition not known in any other glanapterygine or trichomycterid.

INTERSPECIFIC COMPARISONS

The pronounced trend toward reduction in various anatomical features of *Pygidianops* and *Typhlobelus* makes identification of species-diagnostic features challenging. Most of the usual sources of taxonomic information for other siluriforms and other bony fishes are lacking in species of those two genera, which have lost or greatly reduced most of the fins, dark pigmentation, odontodes, and laterosensory canals and pores. Despite that,

species of *Pygidianops* and *Typhlobelus* can be consistently diagnosed by a few traits that are normally used in the systematics of trichomycterids and other catfishes, as well as by various other features that are not usually considered major sources of informative variation in the taxonomy of the group, such as presence of a triangular skin flap at the mouth corner in *P. cuao* and posterior naris absent in *P. magoi* and *T. guacamaya*.

Vertebral numbers seem to be informative for species distinctions among *Typhlobelus*. Although the limited material available for most species does not permit a thorough assessment of intraspecific variation, available data suggest differences so pronounced that it seems unlikely that they will be bridged by more numerous samples, whereas other comparisons raise unresolved questions. The holotype of *Typhlobelus ternetzi* seems to have no more than 60 vertebrae, as counted on a radiograph of the holotype provided by CAS. The diminutive size of the specimen does not allow a clear view of the last few vertebral limits, but the total number certainly does not exceed 60; the only cleared and stained paratype of the species is missing some of the posterior vertebrae and caudal fin, thus making vertebral counts impossible in that specimen. Radiographs of a second paratype of this species (SU 36558) revealed 52 total vertebrae; that specimen has 57 myomeres. *Typhlobelus guacamaya* has 51–53 vertebrae (data from radiographs: $N = 6$, median = 53) and the holotype has 58 myomeres. In contrast, paratype specimens of *T. lundbergi* were observed to have 69–71 total vertebrae ($N = 5$, median = 70), whereas the holotype has 53. This intraspecific difference is indeed surprising and difficult to reconcile. There are no other meristic differences among these specimens, whereas the morphometric variation revealed that the holotype specimen has a substantially shorter caudal peduncle compared to the paratypes. Other relative measures of body length (i.e., preanal, preproctal distances) failed to reveal substantive differences among specimens. Lindsey (1975) found that variation in vertebral number within species tends to be higher in those species having more numerous vertebrae, and that "slim species tend to have higher counts than robust species." Similarly, a large intraspecific range in the total number of vertebrae was observed for the African clariids *Chanallabes apus* (95–117) and *Dolichallabes micropthalmus* (94–116), two catfishes having an extremely elongate body morphology (Devaere, 2005). *Typhlobelus lundbergi* has nearly the highest number of vertebrae and greatest length to width ratio thus far observed among Trichomycteridae. These observations strengthen our confidence that the observed variation is within the normal range for the species. Sexual dimorphism is also a possible explanation for the range of variation in numbers of vertebrae. Urogential papilla absence and variation in papilla size may indicate the presence of both sexes in these samples. However, the delicate condition, small size, and scarcity of specimens makes sex determination by dissection impractical at this time.

In contrast to the situation in *Typhlobelus*, vertebral counts in *Pygidianops* do not vary informatively. The single cleared and stained paratype of *P. eigenmanni* has 40 vertebrae and 10 alcoholic paratypes examined (SU 36557, CAS 11121) have 37–41 myomeres, while the CAS radiograph of the holotype shows no more than 41 vertebrae. The single cleared and stained paratype of *P. magoi* has 40 vertebrae and 39 myomeres, while *P. cuao* has 41 vertebrae and 39–42 myomeres. These observed values indicate broad or total overlap, showing that vertebral counts will not be useful for distinguishing currently known species of *Pygidianops*.

The presence or absence of eyes seems to be stable within species of *Typhlobelus* and *Pygidianops*. All of the numerous specimens of *P. cuao* examined have eyes developed to a similar degree, with no instance of a specimen with vestigial or absent eyes. *Pygidianops eigenmanni* and *P. magoi*, on the other hand, lack eyes entirely, and no known specimen has so much as an eyespot. The four known specimens of *T. ternetzi* and the unique holotype of *T. macromycterus* have small eyes, while all specimens of *T. guacamaya* and *T. lundbergi* lack eyes entirely. The summation of all those observations indicates that the degree of intraspecific variation in eye development in *Pygidianops* and *Typhlobelus* is expected to be minor, and that presence versus absence of eyes can be used

as a reliable guide to species differentiation. One concern in using this characteristic, however, is that eye pigmentation tends to fade after some time in preservative. The eyes in all glanapterygines, but more markedly in the sand-dwelling taxa, are obviously degenerate and seem to have a limited amount of dark pigment. We are confident that the conditions here assigned to each species are not a result of fading, but we do note that eyes in the nearly 80-year old paratypes of *T. ternetzi* are practically faded today.

In the course of making comparisons for this study, we noticed that opercular odontodes may be present in some species of *Typhlobelus*. We first observed them in an undescribed species (currently being described by MDP and J. Zuanon) from the Rio Xingu. In that species, each opercle has one or two closely attached, broad-based, strong odontodes inserted at the posterior end of the bone. The position and shape of the odontodes make them look like a posterior pointed extension of the opercle. This has been confirmed in multiple specimens (including cleared and stained preparations) of the species from the Rio Xingu. We did a careful search for opercular odontodes in specimens available of *Pygidianops* and *Typhlobelus* species, but only found them in *T. macromycterus*. Although details about the structure of the odontodes could not be determined in that species, because they were examined by transparency in the single specimen preserved in alcohol, we are quite sure of their presence in that species. The presence of opercular odontodes is plesiomorphic for Glanapteryginae (they are present in *Listrura* and outgroup trichomycterids), but derived within the clade formed by *Glanapteryx*, *Pygidianops* and *Typhlobelus*, which otherwise entirely lack both opercular and interopercular odontodes as adults. Interopercular odontodes have been recorded for juveniles of *Glanapteryx anguilla*, but seem to disappear with growth (de Pinna, 1989).

Diagnosability of the species recognized herein seems to be well corroborated. The three currently known species of *Pygidianops* are very distinct from one another, and are easily diagnosed on the basis of characters provided in the key. *Pygidianops magoi* is particularly noteworthy in having lost all

fins except for the caudal. This is the most extreme case of fin loss among ostariophysan fishes. Other species in the genus have small pectoral and anal fins. *Pygidianops cuao* and *P. eigenmanni* can be easily distinguished by the presence of eyes in the former and their absence in the latter.

Species distinctions in *Typhlobelus* can be more subtle than in *Pygidianops*. In part, this is due to more limited availability of representative specimens of the former. Also, all specimens of *T. lundbergi* currently known are in a poor condition of preservation, and some of the potentially distinguishing traits could not be verified in that species at present. The most difficult species to diagnose are *T. ternetzi* and *T. lundbergi*. An important distinction between the two species is the presence of eyes (or eyespots) in the former and their absence in the latter. The distinction in the depth of the caudal peduncle fin fold is subtle and the degree of specimen dehydration may impede observation of this trait. Available specimens of *T. lundbergi* no longer have any observable fold, and the condition described and illustrated here was recorded several years ago, when they were in a better state. Despite the difficulty in diagnosing the two species on the basis of external characteristics, we are confident that they are actually distinct. That is because *T. ternetzi* and *T. lundbergi* differ in some additional traits of internal anatomy. The vertebral number, discussed above, is one of them. Another is the shape of the interopercle.

BIOGEOGRAPHY AND PSAMMOPHILY

Species of *Pygidianops* and *Typhlobelus* occupy all three major water types in the Amazon and Orinoco river basins. *Pygidianops eigenmanni* and *T. ternetzi* occur in black water, while *P. magoi* and *T. lundbergi* live in white water. Species from the Río Cuao, *P. cuao* and *T. guacamaya*, occur in clear water, as does *T. macromycterus* from the Tocantins. This diversity suggests that species of *Pygidianops* and *Typhlobelus* are not limited by water type in their range of ecological requirements. That observation, plus the widely divergent localities thus far recorded, indicate that species of the two

genera may be expected to occur throughout the entire Amazon and Orinoco basins, wherever there are suitable sandy habitats.

A psammophilic habit for *Glanapteryx*, *Pygidianops*, and *Typhlobelus* has been presumed on the basis of anecdotal locality information and the extremely reduced morphologies of these species. However, until now, the exact microhabitats of the species of these genera have rarely been observed directly. Myers and Weitzman (1966) conjectured that rock pools below the São Gabriel Rapids, the type locality for each genus, probably had a sandy bottom. Nico and de Pinna (1996) reported capture of *Glanapteryx anguilla* from small forest streams with sandy substrate covered by leaf litter; however, the exact microhabitat occupied was not observed because the specimens were collected using rotenone. Costa and Bockmann (1994) obtained *Typhlobelus macromycterus* from a shallow pool that remained after diversion of a section of the Rio Tocantins during construction of the Tucuruí dam. Those authors did not report the nature of the pool bottom, and given the unusual circumstance of the particular collection, little inference about specific microhabitat conditions can be drawn.

The degree of psammophilic adaptation in species of *Pygidianops* and *Typhlobelus* is remarkable, without parallel in siluriforms and perhaps in any other freshwater fishes. Specialization for life in sand is evident in several morphological traits, such as the loss or reduction of fins, pigment, and eyes. Such reduced or loss features are also commonly observed among troglobitic species (Trajano and de Pinna, 1996; Romero and Paulson, 2001; Trajano et al., 2004). An additional and remarkable specialization observed in these glanapterygine trichomycterids that as yet has no record in the literature is the presence of paired keels along the ventral edges of the abdomen. Each of these keels is formed by a long ridge of stiffened integument, underlain by well-differentiated anterior and medial infracarinalis muscles (fig. 3). The keels extend along the entire ventral margin of the abdomen, ending posteriorly shortly posterior to the anus. That point also marks the beginning of the midventral keel of the caudal peduncle, formed by integu-

ment and adipose tissue. The paired keels are remarkably similar to the metapleural folds of cephalochordates (*Branchiostoma*), and for this reason are here named metapleural keels. Amphioxi are sand-dwelling, and the gross morphological similarity between their metapleural folds and the metapleural keels in glanapterygines is strongly suggestive of an analogous function. Metapleural keels probably serve to stabilize the body while moving in sand. All species of *Pygidianops* and *Typhlobelus*, and no other trichomycterid, teleost, or perhaps even vertebrate possess metapleural keels. The structure is certainly an apomorphic condition, and provides additional evidence that the two genera form a monophyletic group. The metapleural keels become attenuated and dehydrated after long preservation, but we could confirm their presence in all species examined of *Pygidianops* and *Typhlobelus*.

The evolution of habitat preference in glanapterygines seems to follow a trend toward increased specialization to interstitial environments. Species of the most basal genus of the subfamily, *Listrura*, occur in shallow-water leaf-litter deposits underlain by mud or deeper layers of leaf litter. Little is known about the habitats of the species of *Glanapteryx*, but information available indicates that they have been collected in association with leaf litter underlain with sand. By contrast, species of *Pygidianops* and *Typhlobelus* are entirely disassociated from leaf litter, and occupy exclusively clear loose sand. Both *P. cuao* and *T. guacamaya* were found exclusively within the sand substratum, rather than on the sand surface or in the water column. Both were taken together in the top 1.5 m of sand using an aquarium net of 1.0 mm mesh in gently flowing water along the edges of banks and sandbars exposed during an exceptionally low water period. Specimens were discovered only by excavation, followed by carefully picking through the sand, as they did not emerge from the sand even when it was placed on the dry bank. Table 2 shows the composition of a representative sample of the Río Cuao sand substratum in which these species were found. Approximately 64% of the sand particles were greater than 1 mm diameter, with the largest fraction by weight being 1–3 mm

TABLE 2
Summary of Size Composition and Fractionation Analysis of Río Cuao Sand Substratum

Sieve no.	Sieve size (mm)	Weight (mg)	%	Grain size (mm)	Shape	Composition
<10	>2	24.92	9	3–4	angular	quartz (95%), quartzite (5%)
18–20	1–2	148.96	55	>1	subangular	quartz (85%), quartzite (3%), quartz aggregate (2%)
18–25	0.71–1	53.29	20	1	angular	quartz (95%), quartzite (5%)
25–35	0.5–0.71	12.35	5	0.5	angular & subangular	quartz (95%), quartzite (3%), heavy minerals (2%)
35–45	0.36–0.5	7.52	3	0.25	angular & subangular	quartz (70%), quartzite (5%), magnetite & ilmenita (25%)
45–60	0.25–0.36	13.64	5	0.1–0.2	angular & subangular	quartz (35%), magnetite & ilmenita (65%)
>60	<0.25	11.47	4	<0.1	subangular	magnetite (55%), ilmenita (15%), quartz (30%)

diameter. There is a surprising correspondence between sand grain size and body size in these fishes. The maximum width of the larger specimens of these species is within 1–2 mm, suggesting that body width and shape are adaptations to movement in confined interstices, such as would apply to life within the sand. Given their observed preference for the interstitial, rather than open water habitat, and their evident ability to move through the substratum, these glanapterygines could be considered the first vertebrates to be identified as part of the meiofaunal ecological community, the latter defined by Giere (1993) as comprised by benthic interstitial organisms of a size that pass through a standard 0.5 mm or 1.0 mm mesh sieve. Remane (1933), Giere (1993), and others have identified about 20 morphological and life history features commonly found among meiofaunal organisms, all of which are invertebrates and most are marine, that are generally regarded as adaptations to the interstitial environment. Few, if any, meiofaunal organisms have all of these features, yet five and possibly six are found in the species of both *Typhlobelus* and *Pygidianops*: (1) pigment reduced or absent, (2) skin translucent, (3) eyes reduced or absent, (4) paired appendages reduced or absent, (5) increased surface area (e.g., via dorsal and ventral finfolds and metapleural keels), (6) copulatory organ present. The latter feature, presence of a copulatory organ, is conjecture at present because the function of the genital papilla of males and the reproductive behavior of glanapterygines are unknown. *Typhlobelus* species have two additional features, namely (7) length (total) to width ratio greater than 20, and (8) an increased number of segmental units. All of these features are synapomorphic within the Trichomycteridae, and some are shared with other glanapterygines and sarcoglanidines: *Glanapteryx* (1, 3, 4, 7, 8), *Listrura* (7, 8), *Sarcoglanis simplex* (1–3, 5 dorsal and ventral fin folds only). Specimens of *S. simplex* co-occurred with both *T. guacamaya* and *P. cuao* in our collections and displayed a similar behavior upon capture as described above.

Glanapterygine phylogeny indicates that the evolution of the group followed a trend of decreasing dependence on leaf litter and increasing association with sand. It is reasonable to hypothesize that the common ancestor of the subfamily was an inhabitant of extremely small, shallow, and temporary water bodies, marginal to main water courses cov-

ered with vegetation, a microhabitat today occupied only by species of *Listrura* in the region of isolated coastal basins of southeastern Brazil. No species of *Listrura* is known to occur in creeks or rivers, except apparently as stray or colonizing specimens. With increased specialization to sandy environments came the occupation of creeks and even large rivers, where loose sand is often the predominant substratum. The shift to a fully psammophilic habitat may have been the factor that allowed species of *Pygidianops* and *Typhlobleus* to spread over the vast area of the Amazon and Orinoco basins, which includes an extensive network of tributaries with sandy shores and bottoms.

The sister group to the Glanapteryginae is the Sarcoglanidinae (Baskin, 1973; de Pinna, 1998b; Costa and Bockmann, 1994). Most species of the latter subfamily are sand-dwellers (Zuanon and Sazima, 2004), something apparent in their morphology and reduction of skin pigment. Perhaps a single exception to that is *Stenolicmus sarmientoi*, the only sarcoglanidine with heavy, dark integument pigmentation. In any event, both *Ammoglanis* and *Microcambeva*, plesiomorphic members of the Sarcoglanidinae, are strongly associated with sand. That indicates that the subfamily, and perhaps also the common ancestor of the Glanapteryginae plus Sarcoglanidinae, is primitively psammophilic. The question then arises as to whether the leaf-litter environment occupied by *Listrura* and partly by *Glanapteryx* might be apomorphic for those two genera, rather than plesiomorphic for glanapterygines. If that is the case, then the extreme psammophilic specializations of *Pygidianops* and *Typhlobelus* would be simply a continuation of the trend already seen much lower on the tree, at the common ancestor to glanapterygines plus sarcoglanidines. This scenario would be as parsimonious as its alternative proposed above. The possibly exclusive distribution of these species on the continental shield regions might favor the latter hypothesis. Unambiguous resolution of this question requires more complete taxonomic representation. Clearly, much of the biodiversity of the two subfamilies is still undocumented, judging from the rate of descriptions of new genera and species over the past decade. In the near future,

it is reasonable to expect important breakthroughs in the understanding of the evolution of these fishes, as a result of additional forms that are likely to be discovered and added to the phylogenetic hypothesis.

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